

# *Viola suavis* var. *pannonica* (Violaceae), a new white-flowered violet from central Europe

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## Abstract

*Viola suavis* var. *pannonica* (Violaceae) from central Europe is described here as a new variety to science. It is most similar to the blue-flowered *V. suavis* var. *suavis* and the white-flowered *V. suavis* var. *catalonica* and *V. suavis* subsp. *naqshii*, but exhibits differences in several characters, such as petal colour, spur shape, fimbriae length on the stipules, bracteoles position on the peduncle and lamina sinus shape. Although the new taxon is often considered a colour mutation of *V. suavis* var. *suavis*, previous genetic analyses revealed that these white-flowered plants do not arise recurrently at different locations (having multiple origins), but rather form a monophyletic evolutionary lineage. To date, the occurrence of *V. suavis* var. *pannonica* has been reported in the Slovak Republic, the Czech Republic and western Ukraine. In this paper, we report its occurrence in Austria and Hungary. Notes on its etymology, distribution, ecology, origin and hybridization, as well as photographs of the new variety (including the holotype) are also provided.

**Key words:** Pannonia, protologue, taxonomy, variety



Academic editor: Thomas Marcussen

Received: 26 February 2024

Accepted: 23 April 2024

Published: 9 May 2024

**Citation:** Hodálová I, Mered'a Jr P (2024) *Viola suavis* var. *pannonica* (Violaceae), a new white-flowered violet from central Europe. *PhytoKeys* 242: 9–20. <https://doi.org/10.3897/phytokeys.242.121734>

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## Introduction

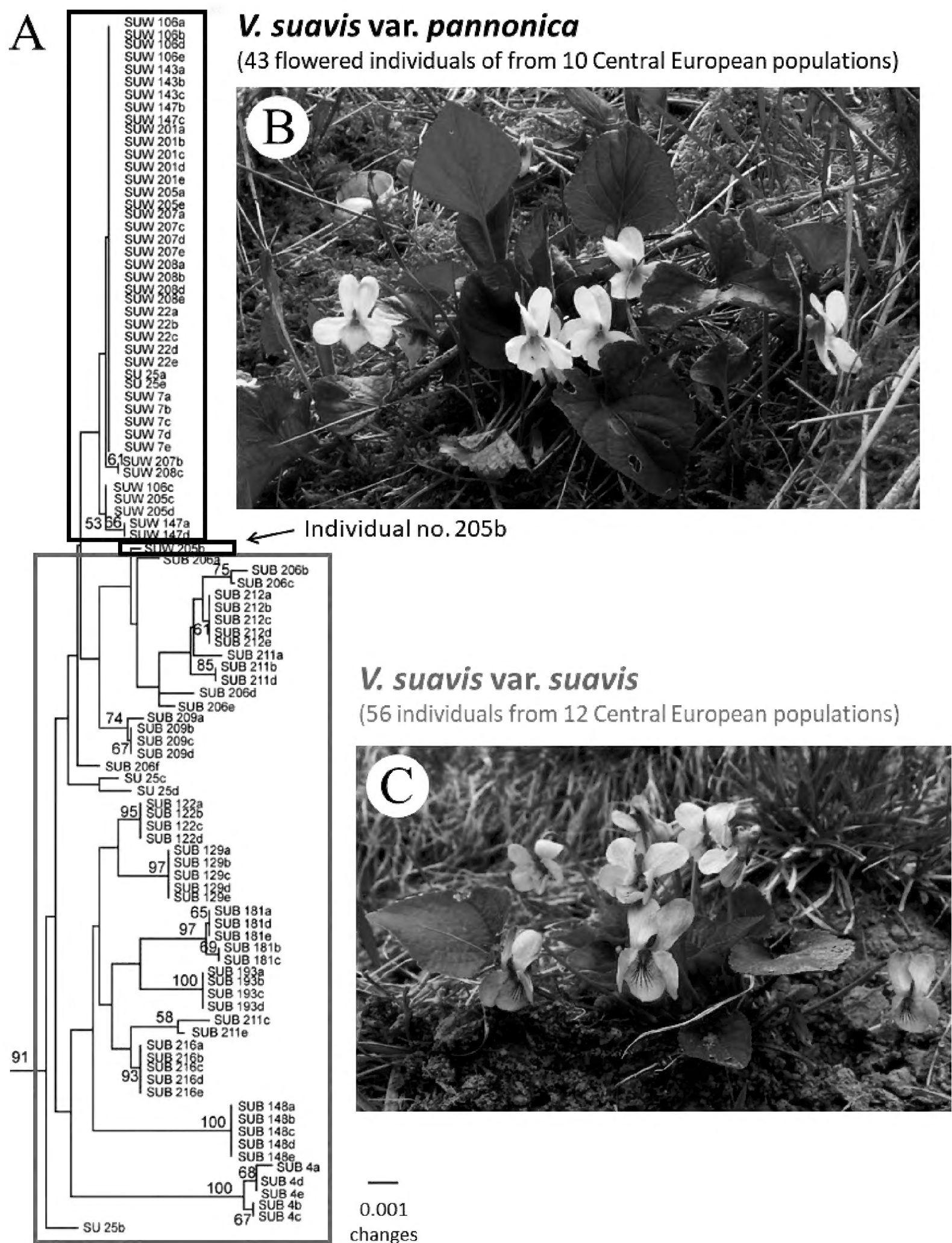
*Viola suavis* M.Bieb. from *Viola* L. subsect. *Viola* (Violaceae) is a perennial herb, differing from related *Viola* species of the subsection in a number of characters: relatively short and stout stolons, long fimbriate stipules, bracteoles located below the middle of the peduncle, glabrous calycine appendages appressed to the peduncle, fragrant flowers (cf. Becker 1910; Gams 1925; Valentine et al. 1968; Kirschner and Skalický 1990; Marcussen and Nordal 1998; Hodálová et al. 2008; Mered'a et al. 2008a, 2008b), and  $2n = 40$  chromosomes (interpreted by different authors either as tetraploid- or (paleo)octoploid; cf. Schmidt 1961; Kirschner and Skalický 1990; Mered'a et al. 2008a, 2008b; Marcussen et al. 2022). The species has been described from northeastern Ukraine (town of Merefa near the city of Kharkiv; the type is deposited in the herbarium of the Komarov Botanical Institute of The Russian Academy of Sciences, Saint Petersburg, Russia; herbarium acronym LE; Marschall von Bieberstein 1819). The distribution range of *V. suavis* extends from the Caucasus and Ural Mountains through the European Mediterranean and sub-Mediterranean regions to

the Iberian Peninsula and Morocco; secondarily, due to cultivation, its area also extends to some parts of western, central and northern Europe (Marcussen and Nordal 1998; Mered'a et al. 2011). An isolated occurrence of the species has been recently reported in Kashmir Himalaya (Ganie et al. 2023). *Viola suavis* prefers dry grasslands, shrublands and open deciduous forests; in addition, it frequently occurs in human-made or human-influenced habitats, such as gardens, parks and cemeteries (Kirschner and Skalický 1990; Marcussen and Nordal 1998; Hodálová et al. 2008; Mered'a et al. 2008b).

*Viola suavis* is a polymorphic species displaying geographically correlated morphological variation, which complicates its taxonomic treatment (Haesler 1975; Marcussen and Nordal 1998; Marcussen and Borgen 2000; Hodálová et al. 2008; van den Hof et al. 2008; Mered'a et al. 2008a, 2011; Ganie et al. 2023). The results of our previous molecular, morphological and chorological studies (Hodálová et al. 2008; Mered'a et al. 2008a, 2008b, 2011) provided strong support for the recognition of four major genetic-morphological lineages of *V. suavis* in Europe, three of which are currently treated in the majority of relevant studies at the subspecific level (e.g., Raab-Straube and Henning 2018+; Nikolić 2020; however, see Marcussen et al. 2022, according to which taxa within *V. suavis* do not merit formal taxonomic recognition): (1) *V. suavis* subsp. *suavis*, occurring in central and eastern Europe (e.g., Mered'a et al. 2008b; Danihelka 2019; Pyšek et al. 2022); (2) *V. suavis* subsp. *adriatica* (Freyn) Haesler (Haesler 1975: 111; bas. *V. adriatica* Freyn 1884: 679), occurring in northeastern Italy, southwestern Slovenia and northwestern Croatia (Mered'a et al. 2011; Nikolić 2020); and (3) *V. suavis* subsp. *austrodalmatica* Mered'a & Hodálová, occurring in southern Croatia, southern Bosnia and Herzegovina and southwestern Montenegro (Mered'a et al. 2011; Nikolić 2020). All three of these subspecies are morphologically clearly distinguishable by several characters, mainly the leaf indument (Mered'a et al. 2008a, 2011).

The detailed morphological pattern of the fourth European genetic lineage (provisionally named *V. suavis* 'Spain') has not yet been elucidated and requires a more thorough study (see Mered'a et al. 2008a, 2011). Populations of this lineage have been found in northeastern Spain and potentially in the adjacent part of France. In the relevant literature, the taxon is regarded as identical to *V. suavis* s. str. (e.g., Valentine et al. 1968; Muñoz Garmendia et al. 1993) or *V. suavis* subsp. *suavis* (e.g., Raab-Straube and Henning 2018+), depending on the taxonomic species concept.

While *V. suavis* subsp. *adriatica* and *V. suavis* subsp. *austrodalmatica* possess only blue to bluish violet petals, *V. suavis* subsp. *suavis* and *V. suavis* 'Spain' have two colour variants: one with typical blue to bluish violet petals (blue variant; Fig. 1C) and one with white petals (white variant; Fig. 1B). The blue and white variants within the given taxa are genetically distinct (Fig. 1A), and in addition to flower pigmentation, they differ in several other morphological characters (Mered'a et al. 2008a, 2008b, 2011; see also Diagnosis). Amplified fragment length polymorphism (AFLP) analyses revealed that white-flowered *V. suavis* subsp. *suavis* and white-flowered *V. suavis* 'Spain' do not arise recurrently at different locations (with multiple origins) but rather form two monophyletic, evolutionarily independent, parallel genetic entities descended from different blue-flowered progenitors in two distinct areas (central Europe and the Iberian Peninsula). Thus, the sympatric occurrence of two colour variants



**Figure 1.** **A** Part of the neighbor-joining tree of AFLP data of 100 central European individuals of *Viola suavis* subsp. *suavis* using Nei and Li distance. Numbers above branches indicate bootstrap support above 50%. Accession labels include taxon abbreviation (SUB – blue-flowered variant (*V. suavis* var. *suavis*); SUW – white-flowered variant (*V. suavis* var. *pannonica*)) and population numbers. Taken from Mered'a et al. (2008a) **B** *V. suavis* var. *pannonica* (Slovakia, Zbrojníky village; photographed by P. Mered'a Jr., 17 April 2013) **C** *Viola suavis* var. *suavis* (Hungary, Visegrád village; photographed by P. Mered'a Jr., 26 March 2011).

within both *V. suavis* subsp. *suavis* and *V. suavis* 'Spain' is most likely the result of secondary contact (Mered'a et al. 2008a).

The white-flowered variant of *V. suavis* 'Spain' from the Iberian Peninsula (Fig. 2) was originally described as *V. catalonica* W.Becker (Becker 1929: 43) from the current public park Jardin del Turó del Putget in Barcelona (Spain)





**Figure 2.** *Viola suavis* var. *catalonica* (Spain, town of Manlleu; photographed by P. Mered'a Jr., 17 March 2006).

(the type is deposited in the Conservatoire et Jardin Botaniques de la Ville de Genève, Switzerland; herbarium acronym G); later, it was treated at the subspecific level [*V. suavis* subsp. *catalonica* (W.Becker) O.Bolòs & Vigo; Bolòs and Vigo 1974: 80] or as the variety *V. suavis* var. *catalonica* (W.Becker) Espeut (Espeut 1999: 16).

The central European white-flowered variant of *V. suavis* subsp. *suavis* (Fig. 1B) has not yet been formally described. In local databases, floras and keys, it is neglected (Farkas 2009), treated as “white-flowered violets of presumed hybrid origin” (Kirschner and Skalický 1990; Suda 2002) or a “white-flowered morphotype” of *V. suavis* subsp. *suavis* (Mered'a et al. 2008b), or considered a *V. suavis* variation (e.g., Michalcová 2011+; Danihelka 2019; FloraVeg.EU 2022+).

Recently, white-flowered individuals of *V. suavis* have been found in a third geographic area, the Kashmir Himalaya (India), and described as a new subspecies, *V. suavis* subsp. *naqshii* (Ganie et al. 2023). This taxon has not been studied morphometrically or genetically. However, it shares several common characters with *V. suavis* var. *catalonica*, such as a hooked spur (Fig. 3A, B) and bracteoles located on the peduncle at a relatively high position.

The aim of this study was to formally describe the central European white-flowered populations of *V. suavis* as a separate taxon at the variety level, based on the results of our previous genetic and morphological studies of the genus *Viola* (Mered'a et al. 2008a, 2011).

## Material and methods

Living plant material was used for morphological studies, including 173 individuals from 16 populations of *Viola suavis* var. *suavis*, 108 individuals from 12 populations of *V. suavis* var. *pannonica* and 42 individuals from 5 populations of *V. suavis* var. *catalonica*. Whenever possible, three measurements were

made for each vegetative character, and two measurements were made for each floral character. The value ranges represent the 10<sup>th</sup> and 90<sup>th</sup> percentiles, with the 1<sup>st</sup> and 99<sup>th</sup> percentiles in parentheses. All measurements were performed at the time of flowering; for character explanations, see Fig. 4. Details on the origin of the material used are given in Mered'a et al. (2008a). Character values for *V. suavis* subsp. *naqshii* have been taken from Ganie et al. (2023).

## Taxonomy

***Viola suavis* var. *pannonica* Hodálová & Mered'a, var. nov.**

urn:lsid:ipni.org:names:77341546-1

Figs 1B, 3C, 5, 6

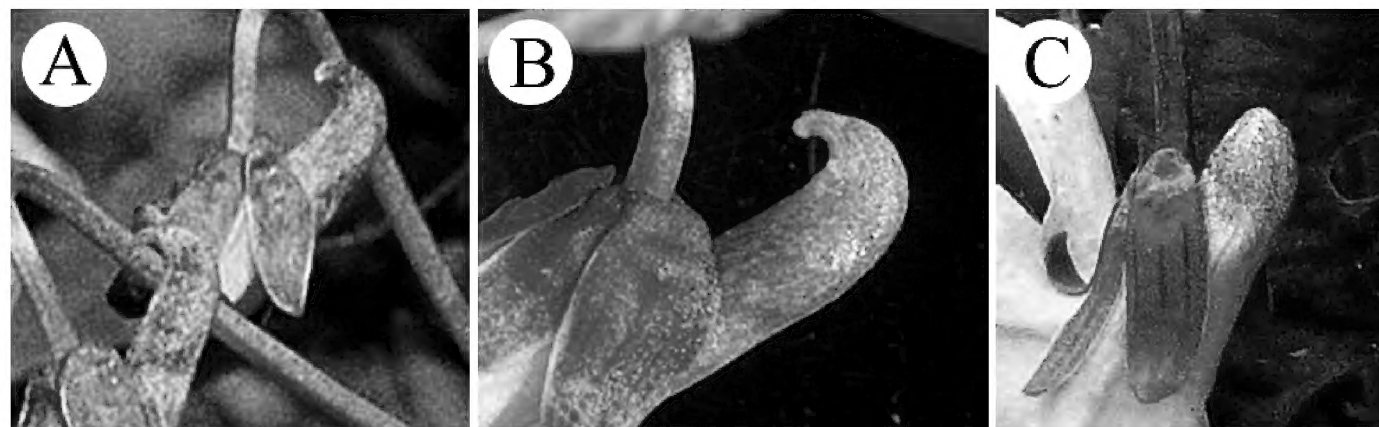
**Diagnosis.** *Viola suavis* var. *pannonica* can be unambiguously distinguished from *V. suavis* var. *suavis* by flower colour: *V. suavis* var. *pannonica* possesses white petals (and a pale to deep violet spur, very rarely whitish or slightly yellow-greenish; Figs 1B, 3C, 6A); *V. suavis* var. *suavis* possesses pale to deep blue or bluish violet petals with a large conspicuous white throat at the base, covering 1/3–1/2 of the length of the lateral and anterior petals (and a pale to deep violet spur; Fig. 1C). In addition to characters associated with pigmentation of the generative and vegetative parts, both varieties also differed in terms of the length of the fimbriae on the stipules ((0.8–)1.2–2.5(–3.1) mm long in *V. suavis* var. *pannonica* vs. (0.4–)0.7–2.0(–2.8) mm long in *V. suavis* var. *suavis*) and by the position of the bracteoles on the peduncle (at (4–)9–29(–40)% of the overall length of the peduncle in *V. suavis* var. *pannonica* vs. (7–)13–42(–52)% in *V. suavis* var. *suavis*).

In addition, *V. suavis* var. *pannonica* differs from the white-flowered *V. suavis* var. *catalonica* and *V. suavis* subsp. *naqshii*, having straight or only slightly upward-curved spur at the top (Fig. 3C) (vs. often distinctly hooked spur (curved up or backwards at the top) in *V. suavis* var. *catalonica* and *V. suavis* subsp. *naqshii*; Fig. 3A, B). Moreover, *V. suavis* var. *pannonica* differs from *V. suavis* var. *catalonica* in terms of the lamina sinus angle ((0–)35–105(–135)° in *V. suavis* var. *pannonica* vs. (–90–)–23–45(–85)° in *V. suavis* var. *catalonica*), lamina sinus depth ((0.1–)0.2–0.55(–1.4) cm vs. (0.3–)0.45–1.1(–1.4) cm), and bracteoles located near the base of the peduncle (at (4–)9–29(–40)% of the overall length of the peduncle vs. at (15–)25–52(–60)% of the overall length of the peduncle). *Viola suavis* var. *pannonica* differs from *V. suavis* subsp. *naqshii* in its longer petiole hairs (0.2–0.6(–0.8) mm in *V. suavis* var. *pannonica* vs. up to 0.1 mm in *V. suavis* subsp. *naqshii*).

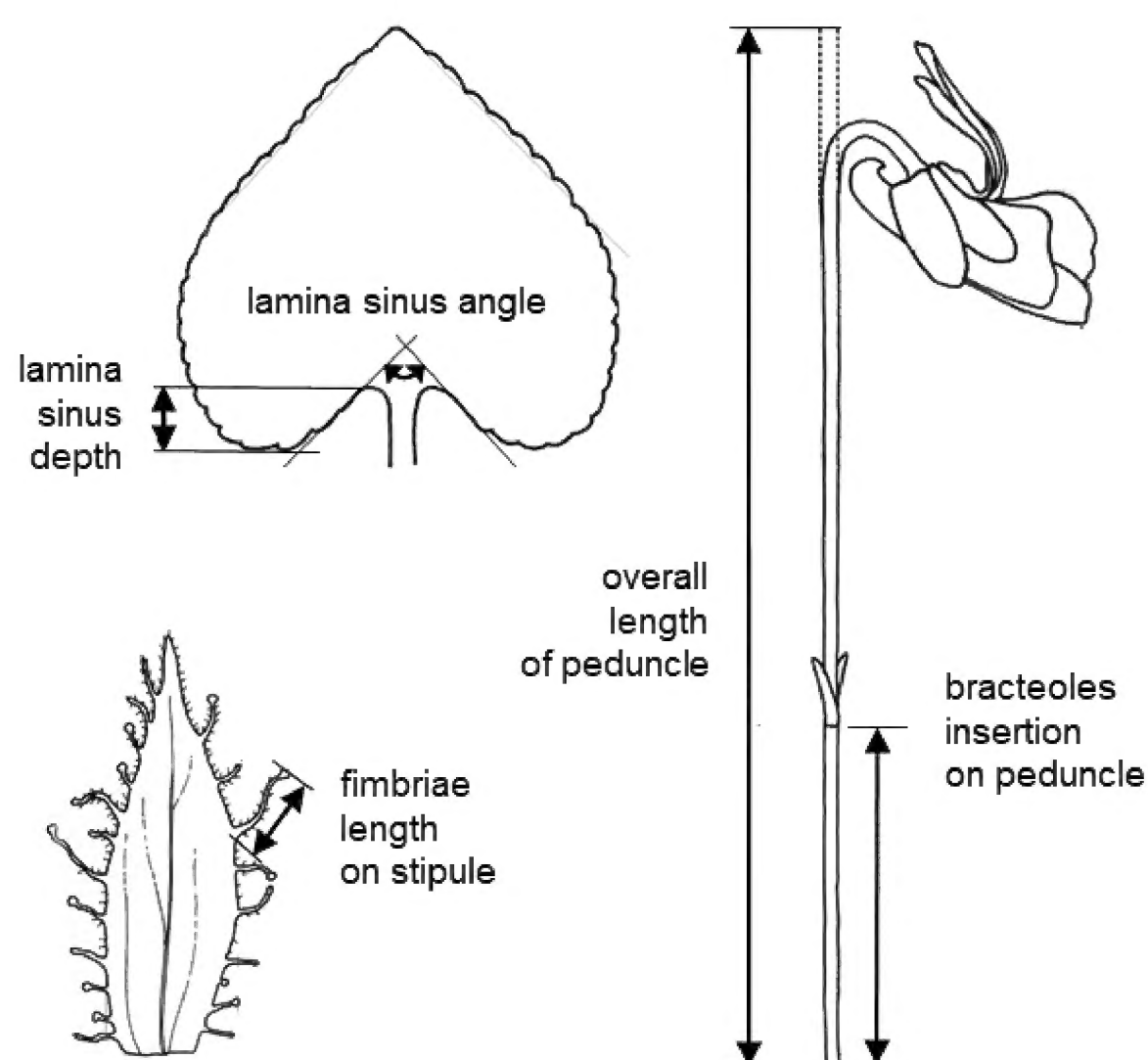
**Type.** SLOVAK REPUBLIC. Devínska Kobyla Hills, Bratislava-Dúbravka borough, Brižite hill, Martina Granca street, 48°11'49"N, 17°01'29"E, elev. 240 m, 1 April 2003, I. Hodálová (Holotype: SAV (SAV0017750; Fig. 5)).

**Phenology.** Flowering from March to April.

**Etymology.** The epithet “pannonica” refers to the geographical region of Pannonia, which is the centre of the hitherto known distribution of the new variety (namely southeastern Moravia in the Czech Republic, northeastern Austria, southern Slovakia, the southern part of Zakarpattia Oblast in western Ukraine, and Hungary; see Distribution).



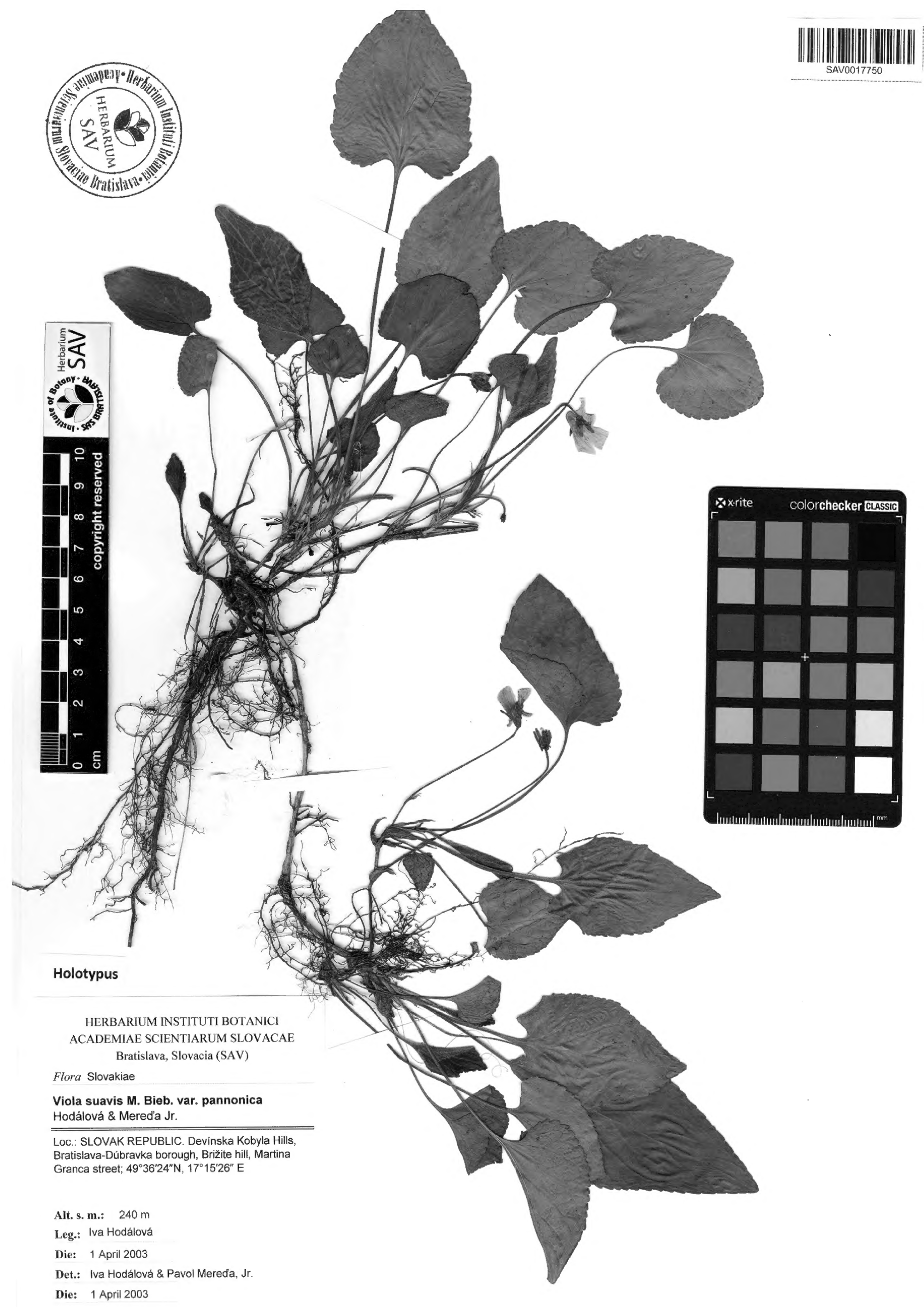
**Figure 3.** Shape of the spur **A** *Viola suavis* var. *catalonica* (Spain, town of Manlleu; photographed by P. Mered'a Jr., 17 March 2006) **B** *V. suavis* subsp. *naqshii* (India, town of Hazratbal; taken from Ganie et al. 2023) **C** *V. suavis* var. *pannonica* (Slovakia, Zbrojníky village; photographed by P. Mered'a Jr., 17 April 2013).



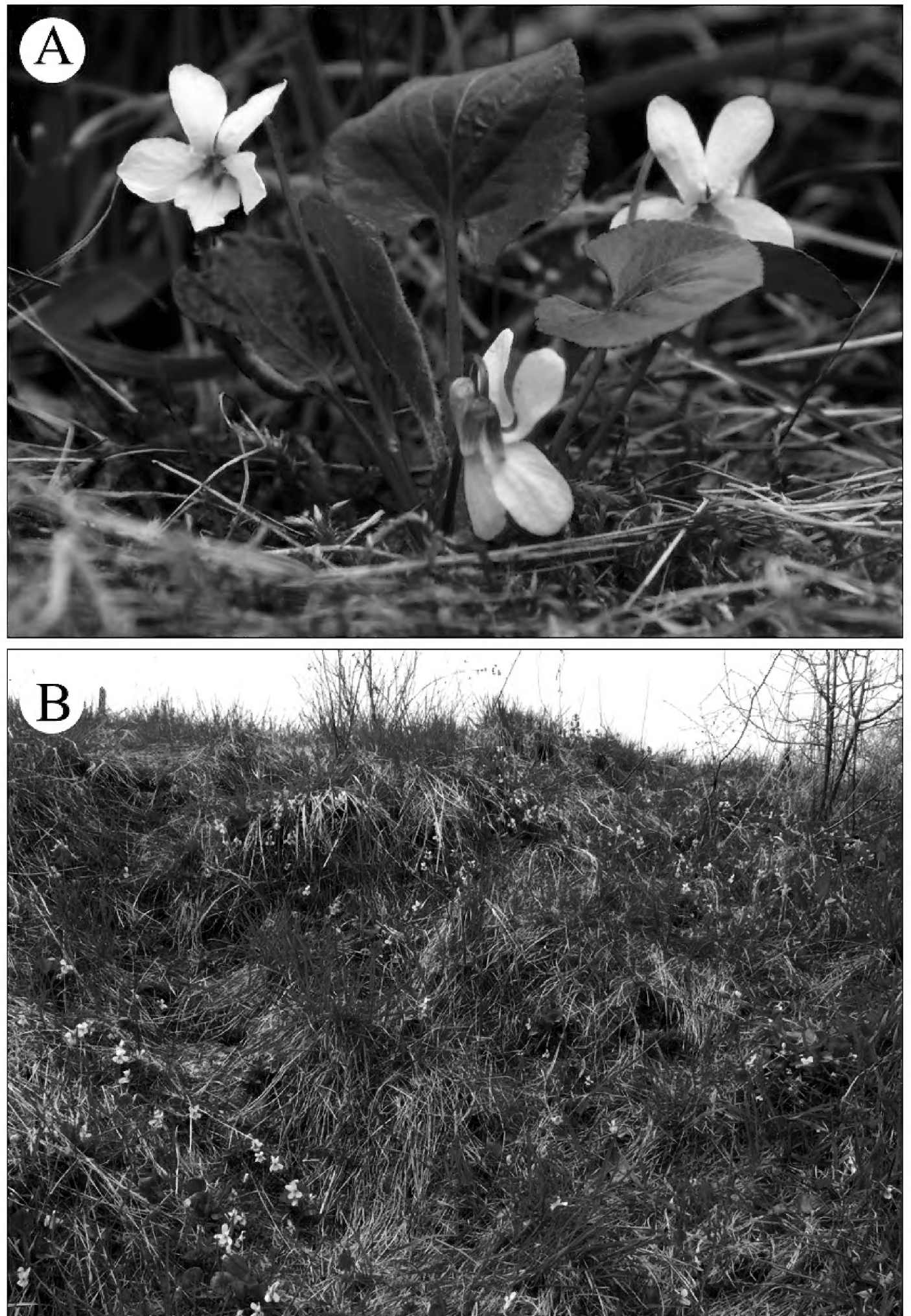
**Figure 4.** Selected morphological characters used in Diagnosis (after Hodálová et al. 2008).

**Distribution.** This variety has been reported in the Slovak Republic (Hodálová et al. 2008; Mered'a et al. 2008a; detailed distribution is given in Mered'a et al. 2008b; see also photographs of *V. suavis* at iNaturalist.org (Photo ID: 202520428, 201130424), nahuby.sk (Photo ID: 257298), <http://flora.upol.cz/fotogalerie/info/9125-Viola-suavis/0-42.html>, and [www.botany.cz/cs/viola-suavis](http://www.botany.cz/cs/viola-suavis)), the Czech Republic (Kirschner and Skalický 1990: 402; Suda 2002: 214 – both papers report the taxon in the note for *V. alba* as “white-flowered violets of presumed hybrid origin”; Hodálová et al. 2008; Mered'a et al. 2008a; Michalcová 2011+; Danihelka 2019; FloraVeg.EU 2022+; see also photographs of *V. suavis* at iNaturalist.org (Photo ID: 151489049, 151956929, 189937608, 201837659, 201843269, 201843461, 201905803, 201906388, 202177193, 202414626, 202716834, 202963367)), western Ukraine (Mered'a et al. 2008a), Austria, and Hungary (both this paper; Fig. 7).





**Figure 5.** The holotype specimen of *Viola suavis* var. *pannonica* deposited in the herbarium of the Institute of Botany, Slovak Academy of Sciences (herbarium acronym SAV).



**Figure 6.** **A** *Viola suavis* var. *pannonica*, plant from the type population (Slovak Republic, Bratislava-Dúbravka borough; photographed by P. Mered'a Jr., 3 April 2008) **B** *V. suavis* var. *pannonica*, habitat (Slovak Republic, Zbrojníky village; photographed by P. Mered'a Jr., 17 April 2013).

This new variety has not yet been reported in the territories of Austria (cf. Fischer et al. 2008) and Hungary (cf. Farkas 2009). Its occurrence in Austria is documented by the photograph from Martin A. Prinz from the town of Traiskirchen, available from iNaturalist.org (Photo ID: 150078107, ut *V. suavis*). In Hungary we found *V. suavis* var. *pannonica* in one location in the northern part of the country: Visegrád village, at the end of Kálvária street, 47°47'09"N, 18°58'20"E,



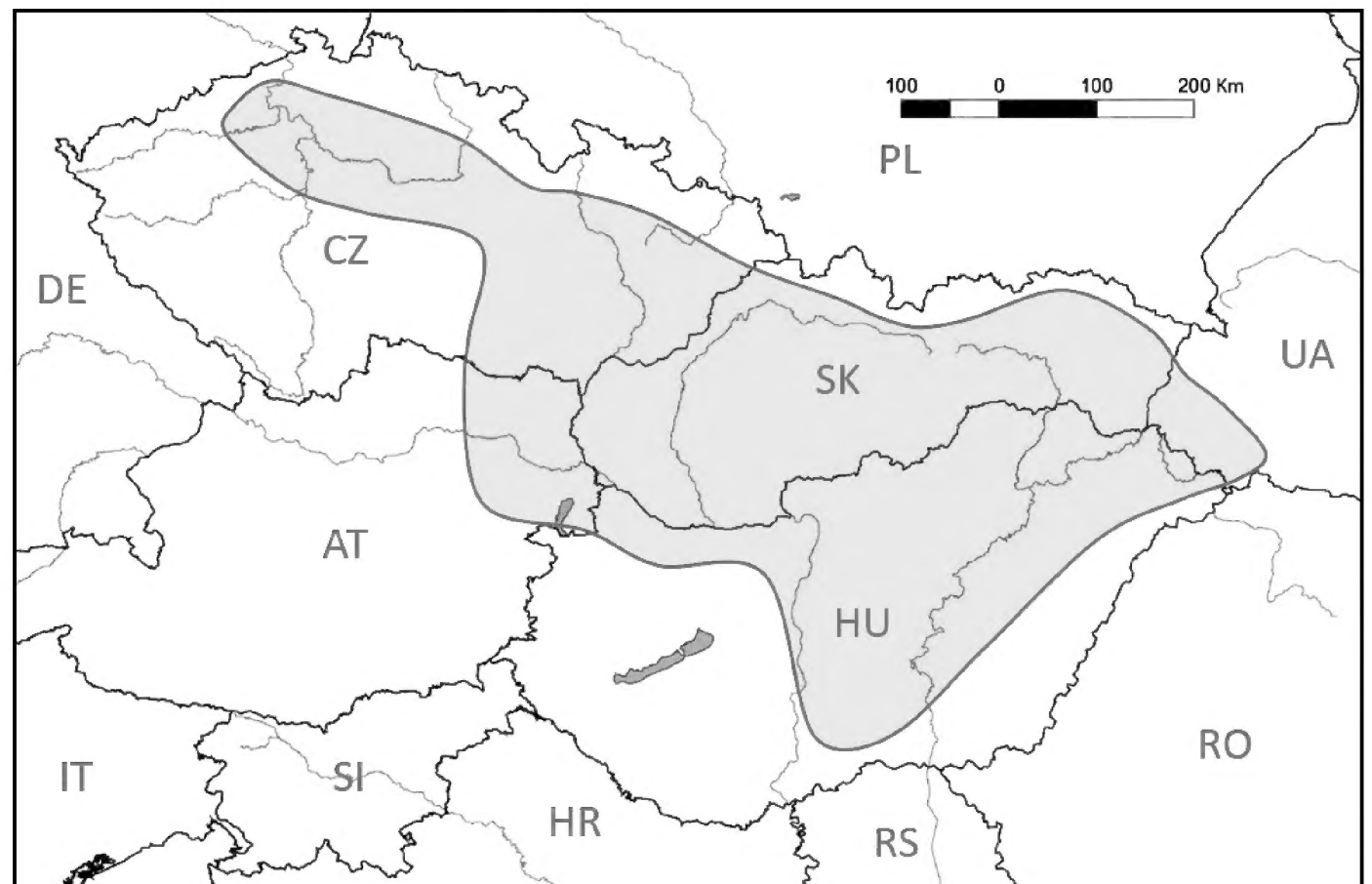


Figure 7. Distribution of *Viola suavis* var. *pannonica*.

126 m, 26 March 2011, P. Mered'a Jr. (photo). In addition, we examined seven other herbarium specimens of the taxon from Hungary (all deposited in the Hungarian Natural History Museum, Budapest, Hungary; herbarium acronym BP; localities are arranged from west to east): near the town of Győr, Csanak, 16 April 1917 and 21 April 1928, S. Polgár (BP), both ut *Viola alba*; Piliscsaba village, Disznófő hill, 6 April 1913, L. Vajda (BP), ut *V. alba*; Budapest city, district II, Hármashatárhegy hill, 12 March 2000, É. I. Bőhm (BP), ut *V. odorata*; Budapest city, district II, Szemlőhegy utca street, 2 April 1917, Á. Boros (BP), ut *V. odorata*; Sárospatak town, 10 April 1933, Á. Kiss (BP), ut *V. alba*; and near the town of Nyíregyháza, Nyíregyházai-erdő forest, 25 March 1927, Á. Boros (BP), ut *V. suavis*. In Hungary this variety has also been documented in two photographs available from iNaturalist.org (Photo ID: 201304283, 203637437). The precise locations of the new variety in the Czech Republic, Austria, Ukraine and Hungary are not yet known, and in these countries, this violet will certainly be more widespread than the data published thus far indicate. The occurrence of *V. suavis* var. *pannonica* is also expected in other central European countries.

**Ecology.** It grows (often in extensive patches; Fig. 6B) mainly in human-made or human-influenced habitats, such as lawns, parks, cemeteries and roadsides in human settlements. It is also commonly cultivated in gardens, from which it is escaping (due to efficient spreading by rooting procumbent stolons and a high seed set per capsule) into their vicinity. In contrast to the nominate variety, *V. suavis* var. *pannonica* only rarely extends into natural and semi-natural habitats outside settlements, where it grows in dry to mesophilous grasslands (Fig. 6B), shrublands, forest edges and open deciduous forests on various soil types (Mered'a et al. 2008a, 2008b).

**Taxonomic notes and hybridisation.** Although in some older studies the authors assumed a hybrid origin of *V. suavis* var. *pannonica* (based mainly on some shared morphological characters with other members of *V.* subsect. *Viola*, namely, *V. odorata* L., *V. collina* Besser, *V. hirta* L., *V. suavis*, and *V. alba*

Besser; cf. Kirschner and Skalický 1990; Suda 2002), molecular analyses clearly revealed that the variety is exclusively derived from the typical blue-flowered central European *V. suavis* subsp. *suavis* (similar to *V. suavis* var. *catalonica*, which is derived from the Iberian blue-flowered *V. suavis* 'Spain'; Mered'a et al. 2008a, 2011). Genetic analyses revealed that *V. suavis* var. *pannonica* has very low genetic variation (Fig. 1A), and most populations in central Europe likely represent the same strain, which was spread in the past by cultivation as ornamentals in gardens and parks and subsequently escaped into the surrounding natural environment. The highly reduced genetic diversity and absence of unique AFLP fragments in individuals of *V. suavis* var. *pannonica*, along with the patterns of fragment sharing and population clustering, clearly demonstrate that the origin of *V. suavis* var. *pannonica* has been recent, perhaps within the last few centuries (Mered'a et al. 2008a).

Although *V. suavis* var. *pannonica* is often sympatric with the blue-flowered *V. suavis* var. *suavis* as well as other species of *Viola* subsect. *Viola* (especially *V. odorata* and *V. hirta*), no morphologically or genetically intermediate individuals have been detected. The absence of hybrids with *V. odorata* and *V. hirta* is not surprising as both these species have a different number of chromosomes ( $2n = 20$ ), and heteroploid hybrids are rare in *Viola* subsect. *Viola* (Mered'a et al. 2008b).

However, the absence of morphologically or genetically intermediate plants between *V. suavis* var. *suavis* and *V. suavis* var. *pannonica* is especially surprising. It is possible that the flower colour in violets may be encoded by a biallelic system where the blue allele is dominant; in that case, colour intermediates might not be possible. However, it is surprising that even in the AFLP analyses, we practically did not identify genetically intermediate individuals, even in locations where the blue- and white-flowered plants were found growing in close proximity or even partly intermingled (population nos 25 and 27, 205 and 206, 208 and 209; Mered'a et al. 2008a and Fig. 1A). An identical situation also occurred for the two colour variants of *V. suavis* in Spain (Mered'a et al. 2008a). The AFLP analyses indicated a possible hybrid origin in only one plant, white-flowered individual no. 205b, which grouped together (although with low bootstrap support) with the blue-flowered plants (Mered'a et al. 2008a and Fig. 1A).

## Acknowledgements

This study was financially supported by the Grant Agency VEGA, Bratislava, Slovak Republic (grant no. 2/0161/21). We thank Jiří Danihelka (Masaryk University, Brno, Czech Republic), Marc Espeut (Prades, France) and Thoman Marcussen (University of Oslo, Norway) for valuable comments on the manuscript.

## Additional information

### Conflict of interest

The authors have declared that no competing interests exist.

### Ethical statement

No ethical statement was reported.

## Funding

This study was financially supported by the Grant Agency VEGA, Bratislava, Slovak Republic (grant no. 2/0161/21).

## Author contributions

Conceptualisation, data curation, methodology, writing: IH, PM.

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## Data availability

All of the data that support the findings of this study are available in the main text.

## References

- Becker W (1910) *Violae Europaeae*. Verlag von C. Heinrich, Dresden, 153 pp.
- Becker W (1929) *Viola catalonica* W.Beck., sp. nova. *Cavanillesia* 2: 43–44.
- Bolòs O, Vigo J (1974) Notes sobre taxonomía i nomenclatura de plantes. I. Butlletí de la Institució Catalana d'Història Natural. Secció de Botànica 38(1): 61–89.
- Danihelka J (2019) *Violaceae* Batsch – violkovité. In: Kaplan Z, Danihelka J, Chrtek Jr J, Kirschner J, Kubát K, Štech M, Štěpánek J (Eds) Klíč ke květeně České republiky, Ed. 2. Academia, Praha, 551–563.
- Espeut M (1999) Approche du genre *Viola* dans le Midi méditerranéen français. *Monde des Plantes* 464: 15–38.
- Farkas S (2009) *Violaceae* – Ibolyafélék családja. In: Király G (Ed.) Új magyar füvészkönyv. Magyarország hajtásos növényei. Határozókulcsok, Aggteleki Nemzeti park Igazgatóság, Jósvalő, 287–290.
- Fischer MA, Oswald K, Adler W, Karrer G (2008) Veilchen u. Stiefmütterchen/*Viola*. In: Fischer MA, Oswald K, Adler W (Eds) Exkursionsflora für Österreich, Liechtenstein und Südtirol. Ed 3. Biologiezentrum der OÖ Landesmuseen, Linz, 430–436.
- FloraVeg.EU (2022+) FloraVeg.EU – Database of the European Flora and Vegetation. [www.floraveg.eu](http://www.floraveg.eu) [accessed 10 August 2024]
- Frey J (1884) Phytographische Notizen insbesondere aus dem Mittelmeergebiete. *Flora* 36: 677–686.
- Gams H (1925) *Violaceae*. In: Hegi G (Ed.) Illustrierte Flora von Mitteleuropa, Band V. J. F. Lehmanns Verlag, München, 585–657.
- Ganie AH, Islam T, Khuroo AA, Tali BA (2023) *Viola suavis* subsp. *naqshii*: a new taxon from Kashmir Himalaya, India. *Phytotaxa* 598(2): 167–172. <https://doi.org/10.11646/phytotaxa.598.2.6>
- Haesler I (1975) Kurze Notiz zur Gattung *Viola* L. Mitteilungen der Botanischen Staatssammlung München 12: 111.
- Hodálová I, Mered'a Jr P, Mártonfi P, Mártonfiová L, Danihelka J (2008) Morphological characters useful for the delimitation of taxa within *Viola* subsect. *Viola* (*Violaceae*): a morphometric study from the West Carpathians. *Folia Geobotanica* 43(1): 83–117. <https://doi.org/10.1007/s12224-008-9005-x>
- Kirschner J, Skalický V (1990) *Violaceae* Batsch. In: Hejný S, Slavík B (Eds) Květena České republiky 2. Academia, Praha, 394–431.



- Marcussen T, Borgen L (2000) Allozymic variation and relationships within *Viola* subsection *Viola* (*Violaceae*). *Plant Systematics and Evolution* 223(1–2): 29–57. <https://doi.org/10.1007/BF00985325>
- Marcussen T, Nordal I (1998) *Viola suavis*, a new species in the Nordic flora, with analyses of the relation to other species in the subsection *Viola* (*Violaceae*). *Nordic Journal of Botany* 18(2): 221–237. <https://doi.org/10.1111/j.1756-1051.1998.tb01875.x>
- Marcussen T, Ballard HE, Danihelka J, Flores AR, Nicola MV, Watson JM (2022) A revised phylogenetic classification for *Viola* (*Violaceae*). *Plants* 11(17): 2224. <https://doi.org/10.3390/plants11172224>
- Marschall von Bieberstein FA (1819) *Flora Taurico-Caucasica exhibens stirpes phaenogamas*, in *Chersoneso Taurica et regionibus Caucasicae sponte crescentes*, Vol. 3. Typis Academicis, Charkouiae, 164 pp.
- Mered'a Jr P, Hodálová I, Mártonfi P, Kučera J, Lihová J (2008a) Intraspecific variation in *Viola suavis* in Europe: parallel evolution of white-flowered morphotypes. *Annals of Botany* 102(3): 443–462. <https://doi.org/10.1093/aob/mcn117>
- Mered'a Jr P, Mártonfi P, Hodálová I, Šípošová H, Danihelka J (2008b) *Viola*les – Fialkovaré. In: Goliašová K., Šípošová H (Eds) *Flóra Slovenska VI/1*. Veda, Bratislava, 80–190.
- Mered'a Jr P, Hodálová I, Kučera J, Zozomová-Lihová J, Letz DR, Slovák M (2011) Genetic and morphological variation in *Viola suavis* s.l. (*Violaceae*) in the western Balkan Peninsula: two endemic subspecies revealed. *Systematics and Biodiversity* 3(3): 211–231. <https://doi.org/10.1080/14772000.2011.603903>
- Michalcová D (2011+) Botanická fotogalerie. [www.botanickafotogalerie.cz](http://www.botanickafotogalerie.cz) [accessed 10 August 2024]
- Muñoz Garmendia F, Montserrat P, Laínz M, Aldasoro JJ (1993) *Viola* L. In: Castroviejo S, Aedo C, Cirujano S, Laínz M, Montserrat P, Morales R, et al. (Eds) *Flora Iberica* 3. Real Jardín Botánico, C.S.I.C., Madrid, 276–317.
- Nikolić T (2020) *Flora Croatica. Vaskularna flora Republike Hrvatske*, Vol. 3. Alfa d. d., Zagreb, 686 pp.
- Pyšek P, Sádlo J, Chrtek Jr J, Chytrý M, Kaplan Z, Pergl J, Pokorná A, Axmanová I, Čuda J, Doležal J, Dřevojan P, Hejda M, Kočár P, Kortz A, Lososová Z, Lustyk P, Skálová H, Štajerová K, Večeřa M, Vítková M, Wild J, Danihelka J (2022) Catalogue of alien plants of the Czech Republic (3<sup>rd</sup> edn.): species richness, status, distributions, habitats, regional invasion levels, introduction pathways and impacts. *Preslia* 94: 447–577. <https://doi.org/10.23855/preslia.2022.447>
- Raab-Straube E von, Henning T (2018+) *Violaceae*. In: Euro+Med Plantbase – the information resource for Euro-Mediterranean plant diversity. <http://www.europlusmed.org> [accessed 1 August 2023]
- Schmidt A (1961) Zytotaxonomische Untersuchungen an europäischen *Viola*-Arten der Sektion *Nomimium*. *Plant Systematics and Evolution* 108(1): 20–88. <https://doi.org/10.1007/BF01297773>
- Suda J (2002) *Violaceae* Batsch – violkovité. In: Hrouda L, Chrtek J. Jr, Kaplan Z, Kirschner J, Kubát K, Štěpánek J (Eds) *Klíč ke květeně České republiky*. Academia, Praha, 207–214.
- Valentine DH, Merxmüller H, Schmidt A (1968) *Viola* L. In: Tutin TG, Heywood VH, Burges NA, Moore DM, Valentine DH, Walters SM et al. (Eds.) *Flora Europaea* 2. Cambridge University Press, Cambridge, 270–282.
- van den Hof K, van den Berg RG, Gravendeel B (2008) Chalcone synthase gene lineage diversification confirms allopolyploid evolutionary relationships of European rostrate violets. *Molecular Biology and Evolution* 25(10): 2099–2108. <https://doi.org/10.1093/molbev/msn157>